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Molluscan assemblages of seagrass-covered and bare intertidal flats on the Banc d'Arguin, Mauritania, in relation to characteristics of sediment and organic matter

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ABSTRACT

The Banc d'Arguin, a non-estuarine area of shallows and intertidal flats off the tropical Saharan coast of Mauritania, is characterised by extensive intertidal and subtidal seagrass beds. We examined the characteristics of intertidal seagrass (*Zostera noltii*) meadows and bare areas in terms of the presence and abundance of molluscs (gastropods and bivalves). To explain observed differences between molluscan assemblages in seagrass and bare patches, some aspects of the feeding habitat (top-5 mm of the sediment) and of food (organic materials) of molluscs were examined. The novelty of this study is that phytopigments were measured and identified to assess source and level of decay (freshness) of organic material in the sediment and to study their importance as an explanatory variable for the distribution of molluscs. Over an area of 36 km^2 of intertidal flats, at 12 sites, paired comparisons were made between seagrass-covered and nearby bare patches. Within seagrass meadows, dry mass of living seagrass was large and amounted to 180± 10 g AFDM m^{-2} (range 75–240). Containing twice the amount of silt per unit dry sediment mass, seagrass sediments were muddier than bare areas; the relative amount of organic material was also larger. The total number of species of bivalves and gastropods amounted to 27, 14 of which were found only in seagrass areas, 4 only in bare and 9 in both types of habitat. Among the three numerically most abundant species, the bivalves *Anadara senilis*, *Dosinia hepatica* and *Loripes lacteus*, the first was numerically most abundant in bare and the other two in seagrass-covered areas. Bare intertidal areas had greater mean total biomass of molluscs (80.5 g AFDM m^{-2}) than seagrass meadows (30.0 g AFDM m^{-2}). In both habitats, the bulk of the biomass was made up by *A. senilis*. Excluding this species, bare mudflats contained on average only 3.1 g AFDM m^{-2} and seagrass meadows 6.9 g AFDM m^{-2}. As compared to previous surveys in 1980–1986, the biomass of *A. senilis* had increased almost 10-fold and *D. hepatica*, previously found in very small numbers, had become the most numerous species. However, the total biomass excluding that of *A. senilis* was similar. Concentrations of phytopigments were similar to those observed at temperate mudflats, indicating that the Banc d'Arguin might not be as oligotrophic as previously thought. Per unit of dry sediment mass, smaller amounts of phytopigments were found in bare than in seagrass areas. Per unit of dry organic material, bare sediments contained most (fresh) phytopigments. This suggests that in seagrass-covered meadows the organic material is more degraded than in bare sediments. Overall, the composition of phytopigments, quite surprisingly, indicated a benthic-diatom-dominated trophic system. Multivariate statistics revealed that patterns of zoobenthic assemblages were correlated with patterns of a combination of four environmental parameters: grain size of the sediment, amount of fresh phytopigments and amounts of leaves and roots of seagrass.

1. Introduction

The Banc d'Arguin, at the western edge of the Sahara, is a large shallow area along the coast of Mauritania. It includes 500 km^2 of intertidal flats with no freshwater inflow from rivers. The entire area of the tropical intertidal mudflats is part of a well-protected national park with little human impact so far (Wolff, 2005). Seagrass *Zostera noltii* grows at about 85% of the intertidal flats (Wolff and Smit, 1990). Previous studies have suggested that the intertidal area of the Banc d'Arguin receives little or no input of nutrients from the oceanic upwelling 100 km offshore (Sevrin-Reyssac, 1993). In addition, there is no evidence for offshore transport of seagrass material (Berghuis et al., 1993). This suggests that the inshore parts of the Banc d'Arguin are isolated and nutrient-limited with slow rates of primary production by phytoplankton and microphytobenthos (Wolff et al., 1993b; Michaelis and Wolff, 2001). This may explain the relatively small standing stocks of benthic invertebrates, 7.6–17.0 g ash-free dry mass (AFDM) per m^2 (Piersma, 1982; Wolff et al., 1993a). These values are at

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the lower end of the range of values reported for intertidal areas in general (Michaelis and Wolff, 2001), where biomass values up to 100 g AFDM m^{-2} are no exception (Heip, 1995).

Seagrass meadows are particularly important habitats for ecological and economic reasons (Costanza et al., 1997) as they, generally, sustain a more diverse and abundant benthic fauna than other intertidal habitats (Orth et al., 1984; Heck et al., 1989; Edgar et al., 1994; Boström and Bonsdorff, 1997; Sheridan, 1997; Siebert and Branch, 2005, 2007). This is because seagrass meadows provide food and shelter, trap and recycle nutrients and stabilise the seabed (Larkum et al., 2006). Earlier studies on the Banc d'Arguin (Wolff et al., 1993a; Wijnsma et al., 1999) confirm that more invertebrate species occur in seagrass meadows than in bare habitat. However, the seagrass-covered areas had smaller zoobenthic biomass than bare areas, as a consequence of the prevalence of the large bivalve *Anadara senilis* in bare areas (Wolff et al., 1993a; Wijnsma et al., 1999; Michaelis and Wolff, 2001).

Although seagrass systems have large standing stocks of primary products, *i.e.* seagrass material, and a fast rate of primary production (Mateo et al., 2006), the products are hardly directly usable by benthic invertebrates. This is shown by stable isotope measurements; benthic invertebrates living in seagrass areas show a distinct algal isotopic signature (Dauby, 1989; Dauby, 1995; Loneragan et al., 1997; Yamamuro, 1999; Lepoint et al., 2000; Davenport and Bax, 2002). Fresh and degraded seagrass is poor food for the following reasons (1) Due to leaking of cell materials during the initial phases of degradation, the remaining material is deficient of inorganic nutrients, particularly N and P, making it less suitable as food (Harrison, 1989), (2) the remaining material is rich in breakdown-limiting phenolic compounds (Godshalk and Wetzel, 1978), refractory polysaccharides and lignin, and (3) as a consequence of the large amounts of organic material in the sediment and high bacterial activity, the benthic environment becomes anoxic, further reducing the rate of breakdown of organic material.

Despite the supposedly oligotrophic nature of the Banc d'Arguin and the poor quality of seagrass as a source of food for zoobenthos, the area is world-famous for its large numbers of (zoobenthos-eating) waterbirds (Smit and Piersma, 1989; Wolff and Smit, 1990). How can it be explained that the relatively small amounts of benthic invertebrates can sustain all these birds? Maybe, the waters are not as oligotropic as expected and primary production of benthic and pelagic algae may be larger than expected. Secondly, a substantial part of the zoobenthos may be able to utilise seagrass as a source of food. In particular, members of the bivalve family Lucinidae are highly specialised in using breakdown products of seagrass (Allen, 1958) and can occur in large densities (see references and data in Johnson et al., 2002).

The first aim of the present study was to quantify differences between seagrass habitat and bare habitat quantitatively and in greater detail than before. To establish the relative richness of zoobenthos in seagrass meadows, we made paired comparisons between the macrobenthic molluscan fauna in seagrass and adjacent bare habitats. Based on earlier work at the Banc d'Arguin (see above) it was predicted that the number of molluscan species was larger and the biomass smaller in seagrass than in bare habitats. The second aim was to find evidence for the importance of phytoplankton or microphytobenthos in the organic material as food for zoobenthos, assuming that fresh alga are an important source of food for many (if not most) molluscs (Page et al., 1992). We, therefore, studied the source and quality of the organic material in sediment. To do this, phytopigments were identified, concentrations determined and the ratio between fresh pigments and their breakdown products used as a measure of the quality of organic material as food for molluscs (Boon and Duineveld, 1996). Due to the accumulation of degradation products of seagrass (see above) it was predicted that the concentration of fresh (algal-derived) pigments in the sediment would be smaller in seagrass meadows than in bare patches. As different green plants have different pigments (Jeffrey and Vesk, 1997), the phytopigment signature can be used to establish the source of organic matter, and thus examine the possible contribution of algae in the food chain. Because seagrass beds trap silt and clay, fine sediments are often associated with a large species abundance (Gray, 1974), and sediment particles can be a major part of ingested materials (particularly for deposit-feeders and scavengers), the importance of sediment grain size as an explanatory variable for patterns in molluscan distribution was also estimated.

2. Material and methods

2.1. Fieldwork and laboratory assays

Our study was carried out in the vicinity of the Scientific Station maintained by the Parc National du Banc d'Arguin (PNBA) at Iwik (19° 52.42′ N, 16° 18.50′ W) between 30 Nov and 14 Dec 2004. As elsewhere on the Banc d'Arguin, near Iwik dense seagrass beds, mainly *Z. noltii*, cover most of the intertidal flats. Sampling locations were spread over an area of about 36 km^2 (Fig. 1) to obtain a representative coverage. At each location (one individual tidal flat) two bare sites and two sites covered in seagrass were selected such that the distance between each bare patch and the nearest seagrass site was always less than 50 m. In this way, five locations resulted in ten bare-seagrass pairs. Data from these 10 pairs (open dots in Fig. 1) were used for the permutational multivariate analysis of variance (see below). In addition, two more locations were visited where only one bare-seagrass pair could be sampled. Finally, one bare and one seagrass site at different locations were sampled (Fig. 1). In total, 13 bare and 13 seagrass sites were sampled, of which 12 bare sites were statistically paired with 12 seagrass sites and analysed accordingly (see below).

To describe patterns in the molluscan fauna in seagrass and bare habitats, three cores per site (internal diameter of 152 mm, thus covering 0.018 m^2) were taken to a depth of 30 cm. The content of each core was sieved through a 1-mm sieve and in the laboratory all (epi) benthic animals were separated from the matrix of seagrass remains

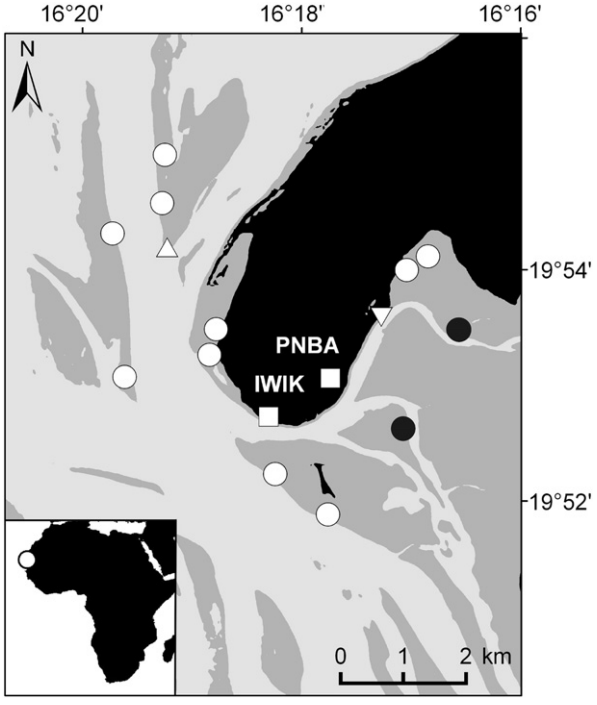

Fig. 1. Position of the sampling sites. The circles represent the sites where paired samples were taken in bare and seagrass areas. Data from the open circles were used in the permutational multivariate ANOVA. For other pairwise comparisons, data from the closed circles were also included. The up and down triangles represent a single seagrass and a single bare site, respectively, and the squares represent the location of the town of Iwik and of the scientific research station of Parc National du Banc d'Arguin (PNBA). Black = land, dark grey = intertidal area, light grey = subtidal area.

and shell fragments. Samples were stored in a freezer at −18 °C until further treatment. Frozen samples were transported to The Netherlands where individual molluscs were identified to species level. Shell lengths were measured with digital callipers to the nearest 0.01 mm (data not used for this study). The ash-free dry body mass (AFDM or organic mass) of each individual was determined by the loss on combustion method after drying the tissues for four days at 60 °C (Honkoop, 2003).

To sample the material that most likely would be ingested by deposit-feeding and filter-feeding (by resuspension) molluscs, samples of only the top 5 mm of the sediment were taken and used for the determination of (1) organic content (2) sediment grain size and (3) phytopigments. At each site two replicate samples were taken. This was done by pressing a 5-mm tall PVC ring (internal diameter 59 mm), which was closed at the top, into the sediment. Then the ring, with a handful of sand or clay from underneath, was removed from the sediment and the excess sand or clay carefully cut off with a knife so that only a 5-mm thick slice inside the ring was left. The material of the slice was as soon as possible frozen at −18 °C. Sediment samples were freeze-dried, carefully ground so that larger parts of seagrass and little shells remained intact but clumps of sediment were broken, and sieved through a 700 µm-sieve to remove seagrass and shells. The particles smaller than 700 µm were homogenised with a mortar and pestle. A subsample of about 0.5 g was taken and (1) organic mass determined by loss on ignition as described for determination of AFDM of zoobenthos.

To determine (2) the distribution of grain sizes, a second subsample of 0.5–3 g freeze-dried sediment, weighed to the nearest 0.01 g was transferred to a 400 ml beaker. Sixty ml demineralised water was added and thereafter 15 ml 35% hydrogen peroxide (H_2O_2). The beaker was covered with a watch glass, left undisturbed overnight and subsequently placed in a hot sand bath and kept at 80 °C for 7 h to degrade organic materials. The beakers were removed from the sand bath cooled to room temperature and about 400 ml demineralised water added to the suspension to dilute remaining hydrogenperoxide. The suspended sediments were allowed to settle onto the bottom of the beaker for at least two days. The supernatant was removed by means of a vacuum pump until ~75 ml of supernatant was left. Just prior to the measurement, the sediment and remaining supernatant were placed in an ultrasonic bath (Branson 5510) and sonified for 10 min. The sample was then quantitatively transferred to a particle size analyser (Beckman Coulter Model LS 230) and 80 ml 0.1 M sodiumpyrophosphate ($Na_4P_2O_7.10H_2O$) was added immediately followed by sonification during 10 min. Then, the grain-size distribution of each sample was determined and median grain size (MGS) and the percentage of silt and clay (particles <63 µm (Folk, 1980)) calculated.

A third subsample of about 0.5 g was taken to characterise (3) the amount and nature of phytopigments. Phytopigments were extracted from 0.5 g of freeze-dried sediment with 1.00 ml 95% methanol buffered with 2% ammoniumacetate and centrifuged. Filtered supernatant was injected into a Waters HPLC and analysed (Witbaard et al., 2001). Pigment-standards were obtained from DHI Water and Environment, Hoersholm, Denmark. In the sediment samples the following fresh pigments were detected and their concentration estimated: chlorophyll *a*, *b*, *c1*, and *c2*, fucoxanthin, 19′-hexanoyloxyfucoxanthin, diadinoxanthin, diatoxanthin, lutein, zeaxanthin, and carotenoids (a mixture of α and β-carotene). In addition, breakdown products of chlorophyll *a* (pheophytin *a*, two unidentified pheophytins, pheophorbide *a1* and *a2* and an unidentified pheophorbide) and one unidentified breakdown product of fucoxanthin were measured. Concentrations were used to estimate the relative amount of fresh pigments (*i.e.* a measure for the amount of fresh alga-material) at the different sites and the ratio of breakdown product to fresh pigments. These ratios can be used as a measure of the quality of the organic material or as a measure of the potential of benthic (micro) organisms to breakdown algal material (Vernet and Lorenzen, 1987; Abele-Oeschger, 1991).

Finally, at each seagrass site, two replicate samples were taken to estimate AFDM of seagrass. A core (internal diameter of 70 mm, covering 0.0038 m^2) was pushed in the sediment and the top 10 cm collected on a 500 µm-sieve. The material retained on the sieve was transferred to a plastic bag and stored frozen at −18 °C. Later, the samples were thawed and all parts of the seagrass, except detrital material, were sorted and separated into either leaves, roots or rhizomes. Tissues were each placed into porcelain crucibles and AFDM determined as described above.

2.2. Statistics

Univariate differences between seagrass and bare areas were analysed by paired *t*-tests, using average values per site for each of the 12 bare-seagrass pairs. Cores were used as replicates. For each variable (zoobenthos, phytopigments and abiotic variables) the direction of the difference could be predicted, so one-tailed *t*-tests were performed with 11 degrees of freedom in all cases.

Using the data collected at each site, the composition of the molluscan benthos and of the phytopigments in sediment and in organic material of the sediment were visualised with non-metric multidimensional scaling (n-MDS), using the software package PRIMER (Plymouth Routines In Multivariate Ecological Research). For the untransformed zoobenthic data, the Bray–Curtis similarity matrix and for log10(X+1)-transformed pigment data, similarity matrices based on Euclidean distances were used. Differences between the two habitats were tested with a one-way multivariate analysis of similarity (PRIMER, one-way ANOSIM (Clarke and Green, 1988; Clarke, 1993). If statistical differences were observed (P<0.05), molluscan species or pigments that contributed most to the difference were identified with the SIMPER-routine in PRIMER (Clarke, 1993) using untransformed benthic and log10(X+1)-transformed pigment data.

Differences in phytopigment and zoobenthic composition between seagrass and bare habitats, among locations (flats) and between sites within each location, were evaluated in more detail by a permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001; McArdle and Anderson, 2001), based on Euclidean distances of the Log10(X+1)-transformed phytopigment-data or on Bray–Curtis distances of untransformed zoobenthic data. To adjust for a limited number of permutations, the Monte Carlo asymptotic *P*-value was used (Anderson and Robinson, 2003). If significant differences between seagrass and bare habitats were found, *a posteriori* pairwise comparisons were made to evaluate the differences. A prerequisite for PERMANOVA is a balanced design. Therefore, only data from the five locations that each contained two bare and two seagrass sites were used in this analysis (sites represented by open dots in Fig. 1). Differences among locations and between sites within each location were not evaluated.

The pattern of the multivariate molluscan data was linked to the pattern of some selected environmental variables measured at each site. These variables were: biomass of seagrass leaves, rhizomes and roots, MGS of the sediment, the percentage of silt and clay and the amount of fresh phytopigments per gram sediment. The percentage of organic material in the sediment was not included because it was highly correlated with both MGS and the percentage of silt and clay. To link the patterns, the similarity matrix of the molluscan fauna (see above) was correlated to the similarity matrix based on normalised Euclidean distances of the selected LOG10(X+1)-transformed variables. The procedure was done with the BIO-ENV procedure in PRIMER (Clarke and Ainsworth, 1993).

3. Results

3.1. Molluscan assemblages

A total of 27 molluscan species was found in the samples and included in the analyses: 13 bivalves, 14 gastropods (Table 1). Also one

Table 1
Composition of the molluscan assemblage in the Iwik area of the Banc d'Arguin in late 2004

Species	Family	Habitat	
		Bare	Seagrass
Bivalvia			
Anadara senilis	Arcidae	170	38
Brachiodontes spec.	Mytilidae	–	8
Musculista senhousia	Mytilidae	–	2
Linga adansoni	Lucinidae	–	4
Loripes lacteus	Lucinidae	42	238
Diplodonta cf. *diaphana*	Ungulinidae	3	35
Cerastoderma edule	Cardidae	–	2
Macoma cumana	Tellinidae	2	–
Tellina spec.	Tellinidae	6	4
Abra tenuis	Semelidae	–	1
Dosinia hepatica	Veneridae	154	222
Tagelus angulatus	Solecurtidae	2	–
Petricola pholadiformis	Petricolidae	1	27
Gastropoda			
Gibbula umbilicalis	Trochidae	–	4
Hydrobia ulvae	Hydrobiidae	1	–
Mesalia mesal	Turritellidae	27	15
Bittium latreillei	Cerithiidae	1	–
Crepidula porcellana	Calyptraeidae	–	13
Muricopsis spec.	Muricidae	–	2
Semifusus morio	Melongenidae	–	1
Columbella rustica	Columbellidae	–	1
Nassarius cuvieri	Nassariidae	–	3
Persicula cingulata	Marginellidae	–	1
Persicula chudeaui	Marginellidae	7	5
Prunum amygdalum	Marginellidae	2	12
Clavatula spec.	Turridae	–	3
Bulla adansoni	Bullidae	–	1
Total number of species		13	23
Individuals per m^{-2} (mean±SE)		596±75	914±80

This table presents total number of individuals of each species and the total number of species found in each type of habitat in all cores combined (n=39 cores of 0.018 m^2 each per type of habitat). For each core the number of individuals per m^2 was calculated and averaged per type of habitat. Sites (n=13 per type of habitat) were used to calculate the standard error (SE).

Table 2
Degree to which different molluscan species contributed to the average Bray–Curtis dissimilarity of abundance between habitats (Contr.=$Diss_i$/Diss*100)

Species	Bare		Seagrass				
	# m^{-2}	% cores	# m^{-2}	% cores	Contr. (%)	$Diss_i$	$Diss_i/SD_i$
Dosinia hepatica	219.4	61.5	316.1	79.5	27.80	21.95	1.20
Loripes lacteus	60.0	23.1	338.9	89.7	26.99	21.31	1.21
Anadara senilis	241.6	82.1	53.9	41.0	21.27	16.79	1.04
Mesalia mesal	38.3	25.6	21.1	17.9	4.35	3.44	0.61
Diplodonta cf. *diaphana*	4.4	7.7	50.0	48.7	4.32	3.41	0.76
Petricola pholadiformis	1.7	2.6	38.3	38.5	4.18	3.30	0.55
Prunum amygdalum	2.8	5.1	17.2	17.9	1.85	1.46	0.37
Crepidula porcelana	0.0	0.0	18.3	7.7	1.54	1.22	0.24
Persicula chudeaui	10.0	15.4	7.2	12.8	1.30	1.02	0.46
Tellina spec.	8.3	10.3	5.6	7.7	1.18	0.93	0.38

The total average dissimilarity (Diss) between habitats was 78.94%. $Diss_i/SD_i$ is the ratio of the contribution of species i to Diss ($Diss_i$) over the within habitat variability (standard deviation, SD_i) of species i (Clarke, 1993). For each habitat the average density per m^2 (# m^{-2}) per species is listed as well as the percentage of cores (% cores) in which this species was found. Total number of cores per habitat was 39 and only species from which more than 10 individuals were found are listed.

individual scaphopod was found but this was not included in the analyses. In addition, several large (mostly predatory) species were encountered on the intertidal flats but did not occur in the samples: the gastropods *Cymbium pepo* and *C. caputvelatum*, *Conus pulcher byssinus*, *Polinices* spec., *Calliostoma dubium* and *Terebra senegalensis* and the bivalves *Brachidontes puniceus*, *Amygdalum agglutinans*, *Goodallia macandrewi*, *Mactra glabrata* and *Paphia dura*, the bivalves occurring only in seagrass meadows. Note that *C. caputvelatum* is identified as *C. tritonis* in a recent study at the Banc d'Arguin (Wolff and Montserrat, 2005). Of the 27 species in the samples, 14 were found only in seagrass areas, 4 only in bare locations and 9 in both types of habitat (Table 1). The average number of species was significantly larger at seagrass (6.83±0.75, mean±SE, n=12) than at bare sites (3.17±0.44 ind. per core, mean±SE, n=12; 1-tailed t-test, $P<0.001$). The total number of individuals per m^2 was also significantly larger in seagrass-covered (915±80) than in bare (596±75) habitats (Table 1; 1-tailed t-test, $P<0.05$).

The composition of zoobenthic assemblages in seagrass and bare habitats was significantly different (ANOSIM, $P<0.001$) and the samples could be reasonably separated in an n-MDS plot (Fig. 2A). Three species accounted for 75% of the observed difference between bare and seagrass habitats, *i.e.* the venerid bivalve *Dosinia hepatica*, the lucinid *Loripes lacteus* and the giant bloody cockle *A. senilis*. All species of which more than 10 individuals were found in the samples explained about 96% of the difference (Table 2). Although occurring in both habitats (Tables 1 and 2), some of these were more common in one habitat than the other. *L. lacteus*, *Diplodonta* cf. *diaphana*, *Petricola pholadiformis* and *Prunum amygdalum* were more abundant in

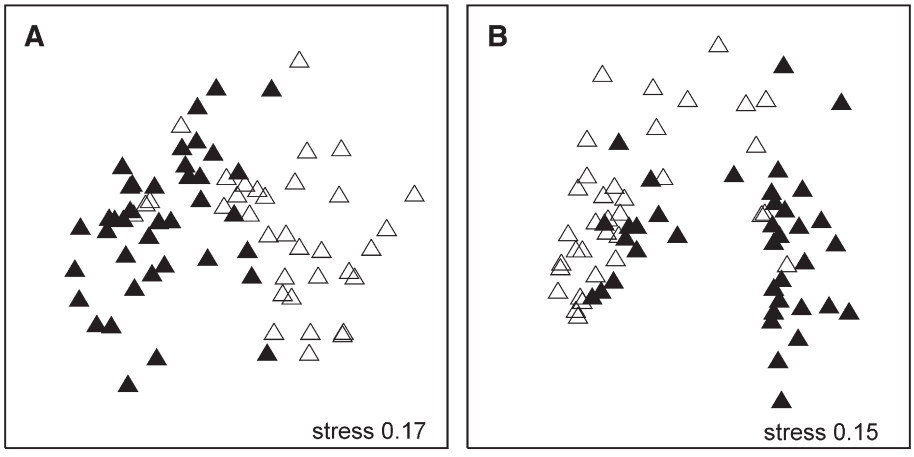

Fig. 2. n-MDS ordinations of (A) the abundance of molluscan species and (B) of the biomass per species of the benthic molluscan assemblages in seagrass and bare habitats. Each replicate sample (n_{total}=39 per habitat type) is represented by one symbol. Closed triangles = bare habitat, open triangles = seagrass habitat.

Table 3
Results of a multivariate analysis of variance of the effects of type of habitat (Type, bare *vs* seagrass), of Location within Type and of Site within Type and Location on (A) abundance and (B) biomass of benthic molluscs

	Source	*df*	MS	*F*	$P_{(MC)}$
A					
Molluscan densities	Type	1	29,660	3.96	0.006
	Location (Type)	8	7486	1.61	0.042
	Site (Type×Location)	10	4661	4.24	0.001
	Residuals	40	1100		
B					
Molluscan biomass	Type	1	19,999	3.23	0.017
	Location (Type)	8	6190	1.12	0.336
	Site (Type×Location)	10	5506	2.63	0.001
	Residuals	40	2096		

$P_{(MC)}$ is the Monte Carlo *P*-value. Cores per site, $n=3$, were used as replicates.

seagrass and *A. senilis* and *Mesalia mesal* in bare patches. *D. hepatica* contributed considerably to the differences between habitats despite a similar average density (Table 2). The contribution was, therefore, due to the fact that in seagrass they were evenly distributed, whereas at bare areas they occurred either in low densities at some and very high densities at other stations. For all species the within habitat variability (SD_i) was relatively large compared to the dissimilarity ($Diss_i$) between habitat resulting in a $Diss_i/SD_i$ ratio slightly larger or smaller than one (Table 2, last column). This picture was confirmed by a more detailed permutational analysis of variance on the balanced subset of zoobenthic data (Table 3A), which revealed that sites within type and location, location within type and the benthic molluscan composition, as found with the ANOSIM-test, was statistically different between seagrass and bare areas. The differences among locations and between sites will not be explored further as our interest only concerns the differences between seagrass and bare habitat.

The species-contribution to the biomass in the two habitats showed again a significant separation of the habitats (ANOSIM, $P<0.001$; Fig. 2B). This difference was mainly driven by one species, *A. senilis*, which attained 77.41 g AFDM m^{-2} in bare areas but only 23.17 g AFDM m^{-2} in seagrass habitat and contributed 72% to the average dissimilarity between habitats (84.19%; Table 4). Other species that contributed to the difference were *D. hepatica* (8.31%), *L. lacteus* (6.28%) and *D.* cf. *diaphana* (3.42%). All other species contributed less than 3% to the difference (Table 4). Also in this case, except for *A. senilis*, the within habitat variability was large, resulting in a small $Diss_i/SD_i$ ratio (Table 4, last column). The permutational analysis of variance showed a similar pattern as for molluscan densities (Table 3). Average AFDM was significantly different between bare and seagrass areas (1-tailed *t*-test, $P<0.05$), amounting to 30.00 g AFDM m^{-2} in seagrass and 80.54 g AFDM m^{-2} in bare areas. *A. senilis* contributed 96.1% and 77.2% to the total AFDM in bare and seagrass habitats, respectively. The biomass of all other molluscs amounted to 3.13 g AFDM m^{-2} and 6.93 g AFDM m^{-2} in bare and seagrass areas, respectively.

Table 4
Degree to which different molluscan species contributed to the average Bray–Curtis dissimilarity of biomass between habitats (Contr.=$Diss_i/Diss*100$)

Species	Bare	Seagrass			
	(g m^{-2})	(g m^{-2})	Contr. (%)	$Diss_i$	$Diss_i/SD_i$
Anadara senilis	77.41	23.17	72.40	60.96	1.75
Dosinia hepatica	1.47	1.99	8.31	7.00	0.55
Loripes lacteus	0.40	1.68	6.28	5.29	0.60
Diplodonta cf *diaphana*	0.10	1.12	3.42	2.88	0.39
Petricola pholadiformis	<0.01	0.86	2.90	2.45	0.35
Mesalia mesal	0.60	0.22	2.10	1.76	0.38

The average dissimilarity between habitats was 84.19%. $Diss_i/SD_i$ is the ratio of the contribution of species *i* to Diss ($Diss_i$) over the within habitat variability (standard deviation, SD_i) of species *i* (Clarke, 1993). For each habitat type average AFDM per m^2 (g m^{-2}) per species is listed. Total number of cores per habitat was 39.

Table 5
Properties of the sediment (median grain size (MGS) and percentage silt and clay) and AFDM of seagrass-tissue in bare and seagrass habitat

Variable	Unit	Bare		Seagrass		*P*-value
		Mean±SE	Range	Mean±SE	Range	
MGS	µm	152.4±16.10	37.5–344.0	77.95±9.27	32.8–169.6	<0.01
Silt and clay	% (V/V)	23.64±4.46	0–76.0	49.09±4.52	7.6–81.4	<0.001
Total AFDM seagrass	g m^{-2}	0		182.1±9.7	75.1–258.4	N/A
AFDM leaves	g m^{-2}	0		54.7±4.4	14.3–80.4	N/A
AFDM roots	g m^{-2}	0		83.5±7.0	33.8–149.3	N/A
AFDM rhizomes	g m^{-2}	0		43.9±3.4	17.6–65.0	N/A

Individual samples were used as replicates ($n=26$ per type of habitat). Sites ($n=13$ per type of habitat) were used to calculate the standard error (SE).

3.2. Seagrass and sediments

Total AFDM of *Z. noltii* in seagrass habitat ranged from 75.1 to 258.4 g AFDM m^{-2} with an average value of 182.1 g AFDM m^{-2} (Table 5). Most of the biomass was found in the roots and rhizomes (Table 5). The mass of the leaves ranged from 14.3 to 80.4 g AFDM m^{-2} with an average of 54.7 g AFDM m^{-2} (Table 5). There was no significant correlation between the AFDM of leaves and MGS of the sediment or the percentage silt in the sediment (Fig. 3). MGS of sediments from seagrass sites was significantly smaller than that from bare sites (1-tailed *t*-test, $P<0.01$, Table 5) and contained significantly more silt and clay (1-tailed *t*-test, $P<0.001$, Table 5). The amount of organic material in the upper 5 mm of the sediment was about 2.5 times larger in seagrass than in bare sediments (1-tailed *t*-test, $P<0.001$, Table 6).

3.3. Phytopigments

The fresh pigments chlorophyll *a* and fucoxanthin dominated the composition of the phytopigments in bare sediments and in sediments collected in seagrass meadows (Table 7A). Log10(X+1)-transformed concentrations of phytopigments were significantly smaller in bare than in seagrass sediments (ANOSIM, $P<0.001$), resulting in a good separation of the two types of habitants in an n-MDS plot (Fig. 4A). The within bare and within seagrass similarities of Log10(X+1)-transformed concentrations per unit sediment were

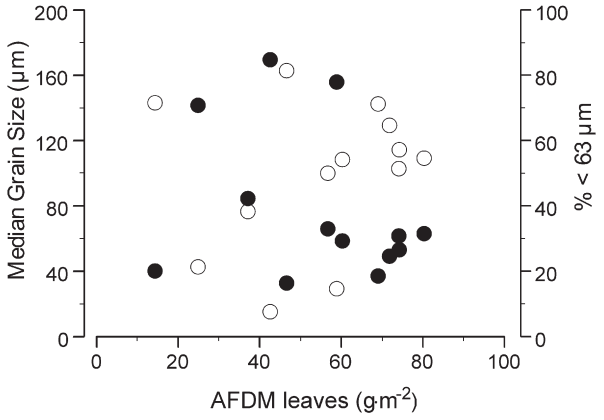

Fig. 3. Relationship between the ash-free dry mass of leaves of seagrass *Zostera noltii* and the median grain size of the sediment (closed circles) and the percentage of particles smaller than 63 µm (open circles). Each data point represents an average value per seagrass site ($n=13$).

Table 6
Characteristics of phytopigments in the organic material from bare and seagrass patches

Variable	Unit	Bare		Seagrass		*P*-value
		Mean	SE	Mean	SE	
OM in sediment	mg g sediment^{-1}	2.39	0.42	6.10	0.67	<0.001
Ratio Chl*a*/OM	mg g OM^{-1}	0.75	0.06	0.56	0.05	n.s.
Fucoxanthin	mg g OM^{-1}	0.16	0.01	0.13	0.01	n.s.
Ratio Lutein/Chl*a*	µg µg^{-1}	0.0039	0.0010	0.0138	0.0016	<0.05
Ratio Chl*b*/Chl*a*	µg µg^{-1}	0.0054	0.0018	0.0137	0.0015	<0.001
Ratio Degr. prod. Chl*a*/Chl*a*	µg µg^{-1}	0.10	0.01	0.13	0.01	<0.05
Ratio Pheophorbides/Chl*a*	µg·µg^{-1}	0.0260	0.0037	0.0253	0.0020	n.s.
Ratio Pheophytins/Chl*a*	µg µg^{-1}	0.0761	0.0077	0.1026	0.0059	<0.05
Ratio Degr. prod. fuco/fuco	µg µg^{-1}	0.25	0.02	0.37	0.03	<0.001
Fresh phytopigments	mg g OM^{-1}	1.05	0.08	0.82	0.06	<0.01

The *P*-value reflects the significance of the difference between bare and seagrass patches. Within habitat differences are ignored. OM = organic material, Chl = chlorophyll, fuco = fucoxanthin, degr. prod. = degradation products, n.s. = not significant. Fresh pigments were chlorophyll *a*, *b*, *c1*, and *c2*, fucoxanthin, 19′-hexanoyloxyfucoxanthin, diadinoxanthin, diatoxanthin, lutein, zeaxanthin, and carotenoids. Degradation products were pheophytin *a*, two unidentified pheophytins, pheophorbide *a1* and *a2*, an unidentified pheophorbide and one unidentified breakdown product of fucoxanthin. Individual samples were used as replicates (n=26 per type of habitat). Sites (n=13 per type of habitat) were used to calculate the standard error (SE).

similar for both habitats and amounted to about 72%, whereas bare and seagrass were 65% similar. Almost all pigments contributed considerably to the difference between habitats but only three (chlorophyll *a*, fucoxanthin and a degradation product of fucoxanthin) each more than 10%, the contribution of all other pigment was less than 7.5% each (SIMPER-procedure, Table 7A). The concentration of all measured pigments was less than half in bare than in seagrass habitat (Tables 6 and 7A). One pigment, 19′-hexanoyloxyfucoxanthin, was only found in relatively small concentrations, on average 0.60 µg g^{-1} sediment, in seagrass and never in bare sediments. A permutational ANOVA on the balanced set of data showed a similar pattern, but differences between bare and seagrass areas were not significant (P=0.093; Table 8). Within each habitat, locations and sites within location were significantly different (P<0.05 and P<0.01, respectively; Table 8), but these differences were not explored any further.

Concentrations of phytopigments per unit organic material showed an opposite pattern. Most fresh pigments, but see below, had smaller concentrations per gram organic material in sediments from seagrass than from bare areas. The concentrations were significantly different (ANOSIM, P<0.001; Fig. 4B). The within bare and within seagrass similarities of Log10(X+1)-transformed concentrations were similar and amounted to about 88%. The average similarity of the habitats was large, 87%. Almost all phytopigments contributed considerably to the difference, the $Diss_i/SD_i$ ratio for almost all pigments was relatively large (Table 7B). The pigments that contributed most to the difference were lutein and chlorophyll *b*, which are main pigments of *Z. noltii* (own measurements) and an unknown pheophorbide. The concentrations of these pigments per g OM (Table 7B) and per unit chlorophyll *a* (Table 6) were larger in seagrass than in bare habitats. A multivariate analysis of variance showed similar differences, though not significant (P=0.064), between bare and seagrass habitat and significant differences between sites within location (P<0.01; Table 8). Locations within habitat were not significantly different (P>0.05; Table 8).

The relative amounts of degradation products of fucoxanthin ($fuco_{degr.}$/fuco) and of chlorophyll *a* ($Chla_{degr.}$/Chl*a*) were significantly larger in seagrass beds than in bare areas. The latter difference was caused by significantly more pheophytins rather than pheophorbides in the organic materials in sediments collected in seagrass (Table 6). The summed mass of fresh phytopigments was significantly larger in bare than in seagrass sediments (Table 6).

3.4. Mollusc-environment matching

The multivariate pattern that emerged from an n-MDS ordination (not shown) of the non-zoobenthic variables (AFDM of the leaves, rhizomes and roots, MGS and the silt and clay fractions and the amount of fresh pigments per g OM) was correlated to the pattern of the abundance of molluscs (using the BIO-ENV procedure, Fig. 2A). The observed maximum matching coefficient (Spearman coefficient, ρ) correlating the two patterns was 0.508 (if ρ=1 than the patterns correlate perfectly, if ρ=0 than the patterns do not match at all). The best grouping of the zoobenthic and environmental patterns was caused by a combination of four environmental parameters: the AFDM of leaves and roots of *Z. noltii*, the MGS and the relative amount of fresh phytopigments in the organic material.

4. Discussion

4.1. Seagrasses, sediment characteristics and the basis of primary productivity

Depending on cover of the sediment by seagrass leaves (Moore, 2004), exposure to waves, and season (Van Keulen and Borowitzka, 2003), seagrass beds are thought to be a sink for fine suspended particles (Agawin and Duarte, 2002). In accordance with this expectation and with results published by others (Edgar et al., 1994), we indeed found finer sediments in seagrass than in bare habitats, but the amount of fine sediments was not significantly correlated with the total amount of seagrass or with the mass of the leaves (Fig. 3). Seagrass-covered sediments contained more organic matter than bare sediments with values being similar to estimates at other seagrass-locations (Edgar et al., 1994; Boström et al., 2006; Qu et al., 2006). Part of the organic material in seagrass areas and in nearby bare patches

Table 7
Degree to which different phytopigments contributed to the average Euclidean dissimilarity of Log10(X+1)-transformed concentrations per (A) gram sediment and (B) per gram organic material (OM) between habitats (Contr.=$Diss_i$/Diss*100)

A	Bare	Seagrass			
Phytopigment in sediment	(µg g sed^{-1}	(µg g sed^{-1}	Contr. (%)	$Diss_i$	$Diss_i/SD_i$
Chlorophyll *a*	16.34	36.37	13.00	4.60	1.56
Fucoxanthin	3.84	9.11	11.97	4.24	1.61
$Fuco_{degr.}$	1.15	3.45	10.43	3.69	1.64
Unknown pheophytin	0.51	1.78	7.49	2.65	1.65
Carotenoids	0.81	1.83	5.88	2.08	1.49
Diatoxanthin	0.43	1.19	5.88	2.08	1.58
Chlorophyll *c1*	0.66	1.51	5.85	2.07	1.52
Pheophytin *a*	0.45	1.33	5.53	1.96	1.45
Chlorophyll *c2*	0.42	0.94	4.20	1.49	1.37
Diadinoxanthin	0.45	0.90	4.13	1.46	1.40
B	**Bare**	**Seagrass**			
Phytopigment in OM	(µg g OM^{-1}	(µg g OM^{-1}	Contr. (%)	$Diss_i$	$Diss_i/SD_i$
Lutein	2.34	7.59	10.26	1.32	1.58
Chlorophyll *b*	2.23	7.84	9.06	1.17	1.75
Unknown pheophorbide	24.55	29.54	8.05	1.04	1.16
Chlorophyll *c2*	22.62	16.10	5.74	0.74	1.33
Chlorophyll *a*	822.55	638.23	5.34	0.69	1.29
Pheophorbide *a2*	5.83	5.43	5.28	0.68	1.38
Zeaxanthin	14.47	12.48	5.17	0.67	0.95
Diadinoxanthin	22.77	16.10	5.13	0.66	1.22
Chlorophyll *c1*	32.14	25.42	5.06	0.65	1.29
Pheophorbide *a1*	9.63	7.80	4.95	0.64	1.40

The total average dissimilarity (Diss) between habitats was 35.41% (per unit sediment) and 12.91% (per unit OM). $Diss_i/SD_i$ is the ratio of the contribution of phytopigment i to Diss ($Diss_i$) over the within habitat variability (standard deviation, SD_i) of phytopigment i (Clarke, 1993). For each habitat the average concentrations (µg g sed^{-1} or µg g OM^{-1}) are listed. Total number of samples (cores) per habitat was 26 and only the ten phytopigments with the largest contribution to the average dissimilarity were listed.

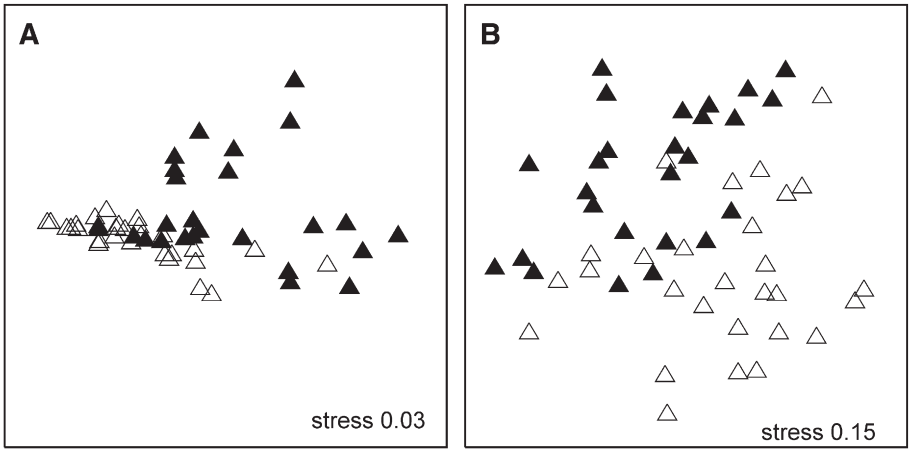

Fig. 4. n-MDS ordinations of all analysed phytopigments (A) per gram sediment and (B) per gram organic material in the sediment. Closed triangles = bare habitat, open triangles = seagrass habitat.

may have originated from seagrass. However, a part of it originated from algae-derived primary products as revealed by the analyses of phytopigments (see next paragraph).

The concentrations of phytopigments found in the sediments from bare and seagrass patches of the Banc d'Arguin were similar to values observed in the productive waters of the Wadden Sea and the Westerschelde estuary in The Netherlands (P.J.C. H., unpubl. data). In both seagrass and bare habitats, the main fresh pigments were fucoxanthin and chlorophyll *a*. The chromatograms of samples collected on the Banc d'Arguin and in the diatom-dominated sediments of the Dutch Wadden Sea (P.J.C. H., unpubl. data) were surprisingly similar, suggesting that diatom production is also important on the Banc d'Arguin. Fucoxanthin is generally used as a marker pigment for diatoms but can also be present in other taxonomic groups (Chrysophyceae, Raphidophyceae and Prymnesiophycea) (Jeffrey and Vesk, 1997; Zapata et al., 2004). However, if chrysophytes and raphidophytes had produced the fucoxanthin, violaxanthin should also be present (Jeffrey and Vesk, 1997), but this was not found. If prymnesiophytes, coccolithophorids or calcite-scaled unicellular marine algae such as *Emiliania huxleyi* had produced the fucoxanthin, 19′-hexanoyloxyfucoxanthin should also have been found (Jeffrey and Vesk, 1997). This pigment was indeed found in seagrass habitats, but only in small concentrations. Thus, in bare and in seagrass habitats, the algae-derived phytopigments must have been produced by diatoms (Qu et al., 2006) and, to a much lesser extent, by pelagic prymnesiophytes. Note that the presence of diatom-produced pigments in sediment of any type of habitat does not necessarily mean that they were produced *in situ*. For example, diatoms produced at bare patches might, via resuspension, be transported to and deposited in seagrass meadows. In addition to the diatom- and prymnesiophyte-derived pigments, part of the pigments in seagrass sediments originated also from seagrass themselves. Characteristic pigments of seagrass are lutein and chlorophyll *b* (Own obs.; Casazza and Mazzella, 2002). They were both present in relatively large amounts in the sediments of seagrass habitats (Table 6) and were the main contributors to the average dissimilarity of the phytopigments per unit organic material between habitats (Table 7B). Therefore, considering both the concentrations of phytopigments and the diatom-like signature of the phytopigments, the standing stock of benthic microalgae must have been considerable.

The amounts of fresh pigments per g of organic material were significantly less in seagrass-covered than in bare sediments. Moreover, the indices of decay of fresh phytopigments, Chl$a_{degr.}$/Chl*a* and fuco$_{degr.}$/fuco (Boon and Duineveld, 1996; Bianchi et al., 2002), were larger in seagrass than in bare habitats, reflecting the more degraded state of organic material in seagrass areas. As concluded above, part of the pigments originated from seagrass plants and, most likely, a major part of the organic materials was refractory seagrass detritus. This all means that, although there is about 2.5 times as much organic material in seagrass sediment, it is of worse quality than in bare patches. Fresh algal material is an important food-source for many benthic invertebrates (Page et al., 1992) and it can thus be stated that for these species the quality of the organic material in seagrass is worse than in bare sediment. However, for the Banc d'Arguin, the importance of fresh algae as a source of food for molluscs is not known. The result of the BIO-ENV procedure showed that the quality of the organic material (among others) might be of some importance but further studies on the diets of molluscs are needed.

The greater proportion of seagrass-derived organic material is inedible for zoobenthos. Therefore, a large part of the organic material produced by seagrass must be metabolised by bacteria (Godshalk and Wetzel, 1978; Harrison, 1989; Kaldy et al., 2006; Küsel et al., 2006). In general, bacteria produce relatively more pheophytins (Bianchi et al., 2000), whereas marine metazoans produce relatively more pheophorbides as main breakdown products of chlorophyll (Robinson et al., 1989; Roy and Poulet, 1990; Bianchi et al., 2000; Goericke et al., 2000; Suzuki et al., 2002; Cartaxana et al., 2003; Szymczak-Zyla et al., 2006). In our study, the amounts of pheophorbides and pheophytins were related to the amount of chlorophyll *a*. The ratio pheophorbide/Chl*a* was not different in the two habitats, but the ratio pheophytin/Chl*a* was significantly larger in seagrass habitats, an observation in accordance with other studies (Kaldy et al., 2006; Küsel et al., 2006). Thus, bacterial degradation of primary products was more important in seagrass than in bare habitats, which again is an indication

Table 8
Results of a multivariate analysis of variance of the effects of type of habitat (Type, bare *vs* seagrass), of Location within Type and of Site within Type and Location on the Log10(X+1)-transformed amounts of phytopigments per gram sediment and per gram organic material (OM) in sediment

	Source	*df*	MS	*F*	$P_{(MC)}$
µg pigm. per g sed.	Type	1	5.103	3.073	0.093
	Location(Type)	8	1.661	5.492	0.020
	Site (Type × Location)	10	0.302	4.321	0.020
	Residuals	20	0.070		
µg pigm. per g OM	Type	1	5.667	2.369	0.064
	Location (Type)	8	2.393	1.316	0.194
	Site (Type × Location)	10	1.818	5.923	0.001
	Residuals	20	0.307		

$P_{(MC)}$ is the Monte Carlo *P*-value. Cores per site, n=2, were used as replicates.

of the poor quality of the organic material in seagrass as food for benthic animals.

4.2. Molluscan assemblages and the benthic food chain

During the first survey in 1980, 12 species of gastropods and 7 species of bivalves were found (Piersma, 1982). During a 1985–1986 study (Wolff et al., 1993a; Wijnsma et al., 1999), 20 species of gastropods and 15 of bivalves were encountered. In our geographically more limited study, 14 species of gastropods and 13 of bivalves were found in the benthic samples. If we take into account the species observed on the surface of the intertidal flats, many of which were large predators, the species richness we found was similar to the results of the earlier studies. There were no substantial differences in sampling effort (except for *A. senilis*, see next paragraph) among the three studies: although the total number of sampling sites differed (28 to 82), per site similar sized samples were taken (0.039 to 0.054 m^2).

In the present study, most of the biomass was contributed by *A. senilis*. Its share exceeded the 60–64% found earlier for the entire intertidal Banc d'Arguin (Piersma, 1982; Wolff et al., 1993a). We found 77.5 g AFDM m^{-2} in bare and 23.3 g AFDM m^{-2} in seagrass areas (96 and 78% of the total biomass in seagrass and unvegetated areas, respectively), whereas Wolff et al. (1987) reported values ranging from 0.0–21.5 g AFDM m^{-2} (average 8.1 g AFDM m^{-2}) for the area around Iwik and Niroumi. It could be calculated that, without *A. senilis*, total mollusc biomass was 3.7–5.7 g AFDM m^{-2} in 1985–1986 (from Table 5 in Wolff et al., 1993a), values are similar to our values, 3.13 g AFDM m^{-2} in bare and 6.93 g AFDM m^{-2} in seagrass areas. Although the sampling design for *A. senilis* differed between our study and the study of Wolff et al. (1993a) the sites in both studies were randomly selected and thus representative for the Iwik and Niroumi area. We, therefore, conclude that the biomass of molluscs (excluding *A. senilis*) remained similar between 1985–1986 and 2004, but that the biomass of *A. senilis* had increased considerably as compared to 1985–1986.

In 1985–1986, the Lucinid *L. lacteus* was the most abundant species and had, after *A. senilis*, the largest biomass (2.6 g AFDM m^{-2}), which was larger than in our study (Table 2). Generally, members of the Lucinidae are important contributors to the biomass in seagrass habitats (Johnson et al., 2002) as they are particularly adapted to utilise seagrass detritus with the aid of endosymbiotic bacteria in their gills (Johnson et al., 2002). *D. hepatica* was the most abundant species in 2004 (Table 2) and after *A. senilis* the species with the largest biomass (Table 4). It is not clear whether this species was found in 1985–1986. Wolff et al. (1993a) found two *Dosinia* species, *D. lupines* and *Dosinia* spec. in very small frequencies implying that they were insignificant contributors to abundance and biomass. In 1980 *D. hepatica* was found in *Z. noltii* meadows but not in bare areas (Piersma, 1982). *Diplodonta* cf. *diaphana* was not mentioned by Piersma (1982), but Wolff et al. (1993a) did observe it outside the quantitative samples.

According to expectation, species composition and abundance were, despite high variation between sampling locations and sites within locations, significantly different between seagrass and bare habitats. As reported by others (e.g. Orth et al., 1984; Heck et al., 1989; Edgar et al., 1994; Boström and Bonsdorff, 1997; Sheridan, 1997; Siebert and Branch, 2005, 2007), more species were found in seagrass than in bare patches. In addition, the total biomass of molluscs without *A. senilis*, was larger in seagrass than in bare patches. However, Wolff et al. (1993a) found the reverse in 1985–1986. Although densities of most species were small, only nine species were found in both habitats, 13 species were restricted to samples taken in seagrass-covered areas and four were restricted to bare areas. For some species the preference for a certain habitat could be expected. For example, the gastropod *Gibbula umbilicalis*, a grazer on epiphytes, was indeed restricted to seagrass. In contrast, the lucinid *L. lacteus*, with a highly reduced alimentary tract (Allen, 1958) and relying largely on symbiotic bacteria for its food-supply (Johnson and Fernandez, 2001; Johnson et al., 2002) was expected to be restricted to seagrass but it also occurred in bare habitat. *D.* cf. *diaphana*, a taxonomically related species but with a fully developed digestive tract and therefore not expected to be limited to a certain type of habitat (Allen, 1958), was found only in seagrass. It is noteworthy that, except for *A. senilis*, due to the large within habitat variability (small $Diss_i/SD_i$; Tables 2 and 4) not a single species was a very good discriminator between habitats (Clarke, 1993).

AFDM of leaves and roots of seagrass, MGS and quality of the organic material in the sediment may all influence (and statistically 'explain') the relative occurrence of these molluscs. However, the correlation coefficient between the multivariate patterns in biota and environmental variables was not very good (Clarke and Ainsworth, 1993), with ρ=+0.504 on a scale ranging from −1 to +1. This leaves room for other variables, perhaps hydrological ones such as wave exposure or shore angle, to explain the variation (Boström et al., 2006).

Considering the presently sizeable standing stocks of *A. senilis*, the intertidal flats around Iwik in 2004 can hardly be called biomass-poor, contrasting the earlier conclusion that the coastal waters of the Banc d' Arguin are oligotrophic and cannot sustain a large zoobenthic biomass (Wolff et al., 1993b; Michaelis and Wolff, 2001). Now that the phytopigment profiles of sediment samples indicate that on the Banc d'Arguin phytobenthos stocks are possibly not that different from that in nutrient-rich temperate waters, we may have to reconsider the above earlier conclusions. The increase in densities and biomass of *A. senilis* warrant explanations in terms of reproduction, the recent series of wet years may have triggered successful recruitment (Wolff et al., 1987) and growth. If so, which primary products supported the growing stocks? The strong increase in numbers and biomass of *D. hepatica*, a filter-feeder that was not found in earlier studies, may indicate that microphytobenthic and phytoplanktonic production now play a larger role in the food chains than ~20 years ago.

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